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THE DISTRIBUTION OF THE COLOR-MARKS OF THE MAMMALIA.¹

BY HARRISON ALLEN, M. D.

The variations in the colors of the hair and the skin are of a character and importance which warrant a systematic study. I have ventured to formulate my impressions on this subject, and while departing in some degree from the directions of approach which zoologists have developed, I have not I trust, stated 'the case without due regard to the views of others on this perplexing phase of observation.

My main object has been to contemplate color marks as the result of nutritive processes controlled by recognized biological forces both in health and disease. I will not hesitate to treat of a perverted growth in the human subject as comparable to a normal growth in any member of the mammalian series.

Statements will be made respecting the distribution of colors of hair, (the superficial color, or rather the effect of the main color of the hair upon the eye being here intended) of the colors of pigment marks on the skin, of localized hypertrophies and atrophies, of vibrissæ, of pilose and naked warts, as though they were co-ordinates of equal value.

I have examined the museums at Philadelphia, New York, New-Haven and Washington. I have consulted the illustrations of works on Natural History and have made extended observations on the domesticated animals especially of dogs, horses, cattle, guinea-pigs and rabbits.

The conclusions drawn at this time have stood the test of repeated re-examinations and while they are not all susceptible of being held as rigid deductions from the premises, they present, I think, a group of tenets which may prove of interest to working zoologists.

The subject of distribution of the hair in the human subject has received attention from D. F. Eschricht² and C. A. Voigt.³

Both writers have taken the new-born child as a standard and have described the directions of the hair in two ways: first as it is

¹ This paper is an elaboration of a portion of an essay which constituted the presidential address at the annual meeting of the American Society of Naturalists, December, 1887.

² Müller's Archiv. 1837, Vol. IV, 37.

³ Denkschr. Wein. Akad. d. Wissenschaft. 1857, Vol. XII, III Abth. p. 1.

observed radiating from certain points, and second as it is seen to converge to certain points.

The following are the main points of radiation. The parietal bone, a short distance to the right of the oboleon, and the axilla. The parietal centres may be symmetrical.

The following are the main points of convergence. The head at the oboleon and directly above the auricle; the face at the inner end of the eyebrow, and at the root of the nose; the neck over the centre of the hyoid bone; the sternum at its upper third; the abdomen at the summit of the bladder; the under surface of the penis at the base; the nape of the neck on each side of the vertebral column; the trunk over the lower part of the coccyx; the side of the trunk; the arm at the insertion of the deltoid muscle; the elbow at the olecranon; the wrist at the head of the ulna; the ilium over the anterior superior process; the thigh at the lower end of the femoral artery; and the ham at the inner border.

It will be found in the course of the ensuing statements that the points of convergences are often found associated with the regions of markings which contrast with the ground-color. Thus the oboleon is the site of brown or black spots in the dog; in the same animal the tan-colored wart is found in black and tan dogs; the centre of the hyoid bone is also the centre of the gular white or gorget in many carnivorous and quadrumanous animals; the sternal point is often white in the horse and dog; the lower end of the back at the sacrum and coccyx is black or brown in ordinarily parti-colored dogs; the insertion of the deltoid is the lower end of the epaulette-region which is frequently of a contrasted color to that of the rest of the limb; the spot over the head of the ulna is in the line of the fringe of the fore-leg in the setter-dog and in some lemurs. The nape of the neck, the root of the nose, the summit of the bladder, the base of the penis, the olecranon, the anterior prominence of the ilium, the femoral point and the inner border of the ham are not found associated with color-marks. These cannot in turn be entirely separated according to Eschricht from being in the line of union of parts which unite late in the development of the foetus. A complicated disposition at the upper lip is held by the same writer to result from the union of the right and left halves at the median line. Some points, as for example the olecranon and the iliac process, answer to bony surfaces which are near the skin. The femoral point is also the region at which the long saphenous nerve pierces the fascia. The point on the

side of the trunk is associated with the naked trunk surfaces of birds, and the colored area in *Indris brevicaudatus*. (See *infra*.)

In men who are notably hairy (the cases of universal hypertrichosis are not here included) the hair is chiefly developed on the breast and the anterior wall of the abdomen at its upper part,—on the region over the trapezius muscle near the scapula— and on the lower part of the loin and the shoulder. In a number of examinations I have made of hirsute men, I have never found the teeth defective unless a disposition to universal hypertrichosis was present. This disposition is shown (in addition to the dental defect) by great shagginess and looseness of contour of the eye-brows. They meet across the inter-orbital space and straggle off toward the temporal side of the forehead. The best marked of the naked places of the body in the hirsute men are the forehead, and the side of the trunk. Eschricht mentions having found but a single example of the trunk being naked at the side. His observations appear to have been made in Copenhagen and may perhaps exhibit a national peculiarity. In America I am sure such naked places are frequently seen. I can confirm Eschricht's statement that hirsute individuals usually have black hair, are of stalwart build and do not of necessity have strong beards or more than ordinary growths from the head.

An instructive analogy can be detected to exist between the naked surfaces on the sides of the trunk and the great lateral featherless spaces (apterylia) of most birds. Above I have invited attention to the fact that in *Indris brevicaudatus*¹ the side of the trunk possesses hair of a different color from that covering the ventre or the dorsum.

The literature of the subject of color-marks is scanty. The papers here given in abstract are of importance.

Th. Eimer² believes the striped forms of the mammalia antedated the spotted, and the retention of color obey phylogenetic laws. He traces the markings of *Viverra* through the varieties of the genus *Canis*. Faint traces of the transverse marks of *Hyena* can be detected in the wolf. The black spot at the root of the tail is mentioned as occurring in all dogs. The presence of a dorsal stripe is mentioned as being commonly present. In vertebrates generally the posterior parts of the body is more strongly marked than the anterior. This is evident in mammals though less marked than in the lower classes.

¹ American Museum of Natural History at New York, No. 260.

² Zool. Anzeiger 1882, V. 685; 1883, 690.

The transverse body stripes are the highest form of development of a body-mark, and succeeds in phylogeny the series of dotted-marks. This order is the reverse of that suggested by Darwin. A paper by G. T. Rope¹ describes two varieties of coloring in the English form of the domestic cat viz: transverse stripes or rows of dots on a white ground and white markings of a more or less longitudinal direction on a black ground.

The following list includes the arrangement of the subject-matter of the present essay.

1. The "break" from the prevailing or ground color compared with the positions at which hair is retained in nearly hairless animals.
2. Brindles.
3. The regions in which color-marks are found regularly disposed. These are: the dorsal line of the trunk; the back of the neck; the dorsi-facial line; the ventre and limbs; the ulnar border of the foreleg; the axilla and pudenda; the "collar;" the regions of the special senses; the sides of the body; the regions of nerve-endings; muscle-regions; regions which are rich in seba and moisture.
4. The effects of age.
5. Bilaterality.
6. Antero-posterior symmetry.

1. THE "BREAK" FROM THE GROUND COLOR, OR PREVALENT COLOR, COMPARED WITH THE POSITIONS AT WHICH HAIR IS RETAINED IN NEARLESS HAIRLESS ANIMALS.—When an animal of a single color changes (even in a slight degree) the uniformity of the tint, the new color will appear in an order definite enough for the variety, species, and sometimes for the family to which the animal belongs. A black, gray or chestnut colored dog when thus changing almost invariably has a white spot appear at one of the following localities: The tip of the tail,² the breast, the dorsal surfaces of the feet, and the tips of the ears. I have observed these changes in the New Foundland dog, the greyhound, the Irish setter and the collie. In the sunbear (*Ursus malayanus*) the prevailing black is relieved by a crescentic whitish-yellow spot on the breast. *Sarcophilus* when varying from its prevalent color exhibits a spot of white in the same region. Horses having white feet and a white

¹ Zoologist, 1881, 353.

² According to Gervais the first white appears at the tip of the tail. G. T. Rope (Zoologist, 1881, 353) states that where only a very minute portion of white occurs, it is most likely to be found on the chest.

star on the breast while the remainder of the bodies are dark are objects of common observation. It cannot be an accidental circumstance that animals that are nearly hairless retain sparse clumps in the same localities. *Rhinoceros lasiotis* is hairless except at the tip of the tail, the dorsal surfaces of the feet and the tips of the ears. *Rhinoceros indicus* shows the same peculiarities to a less marked extent. In *Elephas* the tip of tail is similarly furnished. In the Mexican variety of the so-called hairless dog the same regions named in *Rhinoceros* are alone hairy. In another variety the breast is furnished with an abundant growth of hair. Men, who are more than usually hairy, yet who do not belong to the group of universal hypertrichosis, possess hair on the pectoral region, and are apt to have a sparse growth of hair at the upper margin of the auricle and a similar but separate line of hair along the posterior border, as well as a patch on the loin or near the coccyx in the median line of the trunk.

It may be said that the regions named tend to behave differently from the prevailing disposition in hair-nutrition. In breaking from a uniform color these regions present a contrasted color, and the same regions tend to retain hair which elsewhere for the most part is lost.

But it must be acknowledged that in animals which are for the most part hairless, clumps are seen which do not belong to the above category. These are discussed under other heads. See hair at junction of limbs to trunk, (p. 94) hairs on dorsal line (p. 89) hair at nerve ends. (p. 98)

2. BRINDLES.—In some animals the break from the prevalent color assumes another disposition of a widely spread character. I allude to the plan by which the entire pelt is covered by alternations of black with brown or chestnut: these embrace the “brindles.” The wolf (*Canis lupus*) is often a brindle. Many varieties of dogs *e. g.* some of the mastiffs and bull dogs are brindles. It is often seen in the female of the domestic cat. The prevalent color remaining black the break is seen in dogs to take place to “tan” and to be localized to the feet to the supra-orbital hair clumps and to the hairy wart on the side of the face. The prevalent color being white, black spots are apt to have “tan” margins as is well seen in the fox terrier.

3. THE REGIONS IN WHICH COLOR-MARKS ARE FOUND REGULARLY DISPOSED.—I will now treat of the manner in which the color of a hue which is contrasted to the prevalent color is apt to occur along definite lines or regions of the body.

The Dorsal line of the Trunk. The line of the dorsal spines of the vertebral column (including the head as far as the parietal foramina,¹) is one of the most instructive of these. The black line in the ass and the horse has especially received the attention of Darwin. Prof. Jno. Ryder³ detected a dorsal arrangement of hairs in an embryo of the domesticated cat. It retains the same color in many carnivores. In the domestic cat two pairs of black stripes are often found on either side. In domesticated cattle these are supplanted by a white line. In piebald rats the stripe is commonly black.

Lemur collaris,⁴ has a prevalent squirrel gray color, while the head is black and a black spot is seen at the root of the tail on the dorsal surface. In *Propithecus diadema*,⁵ a conspicuous dorsal line is continuous with a black sacral region and tail. In *Lemur varius*⁶ the same character of dorsal line is seen as in the foregoing animal but is not so marked. In the parti-colored *Indris brevicaudatus*⁷ the region of the back of the sacrum is distinguished from the rest of the fur by being a uniform dull ochreous hue—a hue unlike that met with in any other region of the body. In *Propithecus verreauxi coquereli*⁸ the dorsum near the lower part of the thorax is marked by a dark spot, which is in contrast to the surrounding color. The sacrum and loin are of a dirty gray color. In animals which exhibit spots on the line which are in contrast to the prevalent color the retained colors may be looked upon as persistencies which for some reason have resisted the forces which have displaced the line itself. Such a view is in harmony with Darwin's statement⁹ that dappled and spotted animals were originally striped. One of the numerous forms of *Lemur varius* exhibits a white circle at the base of the tail the prevalent color being light brown. This does not of necessity correlate with the dark sacral spot. But distinctive kinds of marking at the root of the tail in the dog are of the same signifi-

¹ These are persistent in the human cranium near the sagittal suture a short distance in advance of the lamdoidal suture.

² Animals under Domestication pov.

³ Proc. of Acad. of Nat. Sci. 1887, 56.

⁴ American Museum of Natural History at New York.

⁵ Ibid. No. 263.

⁶ Ibid. No. 266.

⁷ Ibid. No. 260.

⁸ Ibid. No. 973.

⁹ Animals under domestication I. p. 65.(Eng. Ed.)

cance as the sacral spot. In *Didelphys* a dark pigment ring encircles the base of the tail. In roan horses a white ring is occasionally found which also encircles the base of the tail.

In *Thylacinus*, *Felis manul*,¹ *Hyena striata*, *Myrmecobius*, and in some of the viverrine genera, the line is interrupted and a number of saddle marks are seen which are best marked posteriorly. In the dog when the black and tan colors are bred out, as in the English setter, the bull terrier and the fox terrier, the dorsal line is retained only at the sacrum and at the root of the tail. It often forms an irregular mark which may extend upon the flanks. In the "Chester reds," a variety of hog bred in Eastern Pennsylvania, black is persistently bred out, yet a small black spot is commonly found at the sacrum. In *Phoca fasciata* a broad white band crosses the trunk at the sacral region.

In *Cercopithecus diana*, the greater part of the dorsal region and all the sacral region are of a red color which extends downward upon the outer surface of the flank.

This disposition is seen in a number of the quadrumana. It appears to be repeated in many dogs (as already mentioned) in which a flank mark is continuous with the sacral spot. The mark may be homologous with the sacral saddle mark of *Thylacinus* and *Felis tigris*.

In a colony of piebald rats observed at the Zoological Garden, Philadelphia, the sacral region was black while the prevalent hue was white.

I will now attempt to explain the persistence of color marks at the region of the sacrum and the root of the tail, though the varieties of the colors themselves are not at present susceptible of demonstration.

In the range of human observation, L. Tait² records the frequent possession—nearly 45 per cent—of a pit, or "sacral dimple," over the sacral region in women.

A. Ecker³ describes the frequent appearance of pits or depressions in the region of the coccyx, in the foetus and in new-born infants. The spot is associated with various pilose conditions. Max Bartels⁴ describes a tail-like formation in man from the lower part of the same region. Virchow⁵ finds the pilose spots co-ordinated with

¹ A. Milne Edwards, *Recherches sur les Mammiferes*, Paris, 1868 to 1874. Pl. 31.

² *Nature*, 1878 XVIII, 481.

³ *Archiv. f. Anthropologie*, 1880, XII, 129.

⁴ *Ibid*, 1881, XIII, 1.

⁵ *Zeitschr f. Ethnologie* 1875, VII 280.

occasional deformity of the sacral spinal processes and he arrives at the conclusion that the sacral pilosity is often connected with attempts at formation of spina bifida. Both Tait and Ecker connect the presence of the sacral depression with the formation of an exerted tail. I make the suggestion that the retention of white, black, tan or lemon colored patches at the sacral and lumbar region is an evidence in tailed quadrupeds of the great activity of nutritive processes between the superficies and deep-seated parts. It is but a step further, and a legitimate step I think, to connect the sacral pigment patches with the subject of sacral tumors which has been so ably elucidated by R. Middeldorpf.¹ This writer traces the congenital sacral tumors to retention-cysts of the neuro-enteric canal of the embryo, as defined by Kowalensky. The canal is the same as the post-anal gut of Balfour. It has been identified in Ascidians, *Amphioxus*, and in plagiostome and teleostean fishes. Should the retention of the pigment patch at the superficies of the region where such profound changes are seen to occur be proved to be associated with minor degrees of interference at the same region, it follows that in the individuals thus marked, minor changes in the sacral elements, and possibly in the condition of the lumbar swelling of the spinal cord, might be sought for.

The Back of the Neck.—The region of the back of the neck including the withers is well known to be often furnished with a mane of long or short hair. It is of interest to note that in a case of *trichosis circumscripta* recorded by Virchow² a distinct pilose growth lay over the region of the third and fourth cervical vertebræ.

As already remarked p. 88 the breast may be hairy in an animal which in other respects is nearly naked. It remains to mention the gnu in which form a pendant growth of hair from the same region is found associated with an animal having short hair—and a long tail furnished with a terminal brush.

The dorsi-facial Line.—The region of the head as far as that of the parietal foramina belongs to the trunk while that in front is distinctive. A white median stripe is commonly found in the region last named in parti-colored dogs. In some varieties a spot of the prevalent color lies directly at the beginning of the trunkal region near the occiput which interrupts the dorsal white line, in the rare instances of its backward prolongation or may be enclosed by it. *Mephitis* may exhibit a white spot on the dorsum of the face especially

¹ Virchow's Archiv 1885, 101, 37.

² Zeitsch f. Ethnologie VII, 279.

in the young. Horses commonly show a white mark, the "star," in the middle of the forehead between the eyes. In *Cercopithecus* a median white spot is often seen on the dorsum of the nose.

The Ventre and Limbs.—The hair of the under part of the trunk is in all animals less thick than that of the upper and is apt to be of a lighter shade of color. The color of the ventre is continuous with the inner sides of the limbs, and with the throat where it is apt to pass in *Quadrumana* to the crown. The account of the color-marks of the limbs cannot be disassociated from that of the trunk. The hair of the outer surfaces of the limbs extends to the sides and dorsum of the trunk and neck, while the inner surfaces extend to the ventre. "Stockings," by which term is meant patches of white color which pass entirely round the manus or pes above the palm or sole, are exceptions to the rule.

The feet of an animal are liable to be of the same color and this color to be black or a break from this color to a contrasted one (see p. 88). In the horse this is notably the case—a bay horse has black feet or exhibits a break from the black color to white. Both fore and hind feet of the Thibetan bear, *Ailuropus melanoleucus*, are black, the rest of the animal being white, with faint shades of brown. The fore foot in mammals is apt to a greater degree than is the case with the hind foot to retain the same color for the arm and the region of the scapula. This is remarkably well seen in *Ailuropus*, in which form the entire fore limb including the shoulder is black, while the hind limb and region of pelvis (excepting the foot) is white. The region of the scapula in many animals is distinctively patterned as is seen in the tiger (*Felis tigris*) and the leopard (*Felis pardus*). In the dog the prevalent color of the neck and the trunk is rarely continuous over the region of the scapula, which is usually of the contrasted color. The spots on the side of the trunk in white dogs appear to be arrested by the region of the scapula. A post-scapular spot of an opposed color is commonly seen in dogs.

P. Michelson¹ describes cases of *trichosis circumscripta* in which clumps were found above and below the region of the scapula but not upon it. I have often found similar clumps in hirsute men. In the horse and its allies the stripes when sparsely distributed are confined to the region of the scapula or lie in front of it. The region of the scapula is apt to be white in *Pecora*. The region of the shoulder, *i. e.* the region of the humero-scapular joint, is separately

¹ Virchow's Archiv. 1883, Vol. C. 66.

marked in a number of diverse forms. In many bats a tuft of white color distinguishes this region. In the llama, camel and bison shaggy tufts of hair adorn it. *Cynocephalus hamadryas* exhibits on both shoulders conspicuous growths of hair which extend backward. In a specimen of *Colubus guerza*¹ the shoulder was found furnished with an epaulet of long white hair. In other examples of this species the epaulet extends backwards. B. Ornstein² describes an instance of *trichosis circumscripta*, in an adult man in which a clump of hair was found on both shoulders.

In *Quadrumana* the colors of the limbs are apt to be differently disposed from the arrangement in quadrupeds. In *Lemur catta* the colors are much like those in lower animals and in all varieties white stockings may be seen in the fore arm and leg. The inside of the limb is apt to be of a lighter color than the outer.

With this qualification I think I may say that the outer surface and anterior surface of the thigh to a point answering to the proximal third or fourth of the tibia is differently colored in *Quadrumana* from the leg and the foot. This is noticeable in *Indris breviceaudatus*³ and *Propithecus verreauxi-coquereli*.⁴

The manus is commonly black in *Quadrumana*. In *Indris breviceaudatus*⁵ the outer side of the arm is black, while the entire forearm is white.

In the figures of Audebert⁶ the separate color marks of the limbs often correspond to the regions of manus, fore-arm, arm, pes, leg and thigh especially for the outer surfaces. From the well known artistic abilities of Audebert these figures may be accepted as authoritative.⁷

The ulnar Border of the Foreleg.—The ulnar border of the foreleg often displays hypernutritive characters. The disposition is not confined to the mammalia. In this class the growth is most likely a survival of the natatorial form of foot and is at best an adaptive

¹ Am. Mus. No. 298.

² Arch. f. Anthropologie 1886, 507.

³ Am. Mus. No. 260.

⁴ Ibid. No. 973.

⁵ Ibid. No 260.

⁶ L'Histoire Naturelle des Singes, des Makis, et des Galéopithèques, 1800.

⁷ C. F. Maynard (Quarterly Journ. Boston Zool. Soc., 1883, II, 18) states that in the variety of bear (*Ursus Americanus*) met with in Florida "brownish lines" are seen "starting from the point of each shoulder and extending down the legs on the inside." This disposition is certainly exceptional.

effort to extend a fold of skin from the sides of the limb. A skin-fold is demonstratable in *Menopoma* (where it is supplied by a branch of a nerve) as well as in *Emys* and its allies. It is the beginning of the hair-covered membrane in the flying squirrel (*Sciuropterus*) and in *Belideus*; it is enormously displayed in the bat.

The long fringe on the ulnar border of the fore-arm in the setter dog may be named as an example of its occurrence in a terrestrial mammal.

The fold corresponding to it is not so evident in the hind leg—where it would naturally be sought for on the inner border. The line of feathers seen in some varieties of the pigeon and of the domestic fowl on the outer border of the leg may be associated with a similar proclivity to that above named.

In a case of *trichosis circumscripta* recorded by B. Ornstein¹ in an adult male a growth of hairs was found on the ulnar border of the fore-arm of both sides.

In some species of *Quadrumania* the hair of the arm and the fore-arm inclines toward the elbow. Wallace² and Darwin³ describe this arrangement in connection with the use made of it by the animal in shedding the water falling upon the flexed limb. That the hair in *Hylobates agilis* should be directed toward the wrist is evidently an aberrant arrangement if we are to follow the distribution of the lanugo as outlined by Eschricht and Voigt.

A marked instance of growth of the hair from ulnar border of the fore-arm and the corresponding border of the arm is met with in *Propithecus verreauxii-coquerelii*.⁴ A long brilliant fringe of orange and white colors equals in width the arm at its greatest diameter.

The Axilla and Pudenda.—The presence of hair in the axilla and pudenda in man is not without interest in connection with the pilose regions of the newly born infant. It will be noticed that both Eschricht and Voigt separated the pudenda and the entire perineum from the rest of the body.

In *Lemur varius*⁵ the prevalent color being a light brown the perineum is black. The axilla is often of the same color as the inside of the entire fore-leg in *Indris brevicaudatus*.⁶

¹ Arch. f. Anthropologie, 1866, 507.

² On Natural Selection, 344.

³ On Descent of Man. Am. Ed. I. 185.

⁴ Am. Mus. No. 973.

⁵ Ibid. No. 268.

⁶ Ibid. No. 260.

It would appear that retention of hair at both junction of the fore and hind leg with the body is in some way connected with secretion and with retention of heat at these localities. (See p. 94.) The black stripe which is well defined in many examples of *Lemur varius* may extend as far as the patella or a little distal of that bone. In the case of the child exhibiting circumscribed trichosis reported by H. Ranke¹ a large pilose patch occurred at the front of the patella and the upper part of the leg to its distal side. Two small patches were found in line with the front of the thigh.

The position of the pilose marks above mentioned can be consistently placed in the same category as the thigh marks in the lemurs.

The Collar.—The region of the head is distinguished in some of the more specialized mammals by a transverse band extending from the vertex down over or near the auricle (commonly in front of this appendage) and is variously dispersed on the neck. It is an interesting region since it affords some of the most striking superficial color-marks of the Quadrumana and is the probable precursor of the hair of the crown of the head and of the beard in man.

In the figures of Eschricht's and Voigt's papers on the lanugo already quoted, the outlines of the region of the color are clearly determined.

In many species of Quadrumana the region of the vertex of the head to near the occiput, the auricle, the region below the auricle and the throat and submaxillary regions are white. This disposition is conspicuous in *Hylobates lar*.² In *Colobus guereza*, the prevalent color being black, a white color is disposed as above and extends down the neck to the clavicle. In *Colobus vellerosus* the collar is white and includes the gular region. In *Cercopithecus diana*, the white collar is interrupted by black at the side; the chin is furnished with a white goatee. The prevalent color is a squirrel gray. In *Cebus hypoleucus* the collar is continuous down the neck and is continuous with the white scapular region and with the outside of the arm to a little below the elbow. The prevalent color is black.

In *Lemur varius*³ the ears, retromaxillary region and the neck uniting the head lines, are white. In *Lemur albifrons*⁴ a white band extends from the white crown over the head and thence to the neck.

¹ Archiv. f. Anthropologie, 1883, 339, XIV.

² American Museum of Natural History, No. 953.

³ Ibid. No. 266

⁴ Ibid. No. 275.

In *Lemur catta*¹ the prevalent color being squirrel gray, the white color between the eyes unites with the color round the eyes and thence passes to the front of the neck. In another individual of the same species (No. 268) the crown remains black, while the rest of the collar is white. In *Phoca fasciata* a white band encircles the head and neck at the region of the auricle.

It will be seen from these examples that the color of the vertex which may be defined as the crown of the head, excepting the margin near the occiput, is often white; that this color tends to pass down over the region of the ear to the neck, where it may unite with the white of the ventre and embrace more or less of the arm. With the exception of *Phoca fasciata* I have not met with this color mark outside of the Quadrumana. Within the group last named the band appears to be homologous with the hair of the crown and the whiskers of the human subject. In the Saki the color is black in this region and inclines forward to the submandibular growth or the beard proper.

The abruptness of termination of the white patch on the crown as it approaches the occiput, appears to relate to the limitation of baldness of the human subject, and explains the common retention of hair at the line of the occiput. The occiput is under the control of the causes which maintain the body color as distinct from that of the rest of the head.

The Regions of the Special Senses—In addition to the dorsi-facial stripe in the carnivores and the “collar,” the mammalian head displays a very noteworthy feature in the retention of a contrasting color to the prevalent one of the body, about the nostrils, the eye-lids and the auricles. Such a style of coloration is typically represented in *Ailuropus melanoleucus*, in which form the body color is a dull white. According to Darwin² the Himalayan rabbit at birth is white, but in the course of a few months it gradually assumes dark eyes, nose, feet and tail. The circumpalpebral black is found in many animals when the ear is imperfectly pigmented, as in *Didelphys* and *Solenodon*. In *Nycticebus javanicus* the circle is brown. In *Nyctipithecus* and *Loris* the two circumpalpebral circles unite in a median dorsal line. In *Nasua* the circle is white. In *Cercopithecus aethiops*, *C. collaris* and *C. fuliginosus* the eye-lids are white. In many dogs which are otherwise black or black and tan—a conspicuous black

¹ Am. Mus. Nat. Hist. 270.

² Animals under Domestication I, 109.

patch surrounds one eye and includes one or both ears. Such are fox terriers, bull terriers and bull dogs. The two patches of circumpalpebral black may interrupt the dorsi-facial white stripe as is seen occasionally in the beagle.

Both the eyelids and the auricle may be included in the same patch of black as is seen in many dogs especially in pointers. The same is noticed in the Japanese dog. This disposition leads the observer to note that the same black patch may extend still farther backward and be found on the sides of the body. A typical example of such an arrangement is seen in *Myrmecophaga jubata*. In *Myrmecobius* the circle extends backward in a stripe. I have seen a similar stripe in the Scotch collie. In *Procyon* the patch is for the most part infra-orbital and extends backward to include the ear. In one of the many varieties of *Mephitis* the ear and auricle are included in a line of black, while the rest of the head is furnished with white longitudinal stripes; more commonly, however, the entire head is black except a jugal stripe which is white and extends down on the sides of the trunk but inclining toward the dorsum as in *Myrmecophaga*. When the auricle is black the tip may be furnished with a pencil of white hairs which suggest the reversion to the plan of coloration described on page 88.

The region of the nostrils or the muzzle is pigmented black in most mammals an exception being found in the *Quadrumana* as in *Semnopithecus nasalis*.

It is interesting to find that in the bull terrier the black may disappear in whole or in part from the muzzle.

The special organs containing as they do black pigment often appear to determine retention points of the same color at the periphery.

The breaks in the circumpalpebral color determine the disappearance of the color from the region in hairless animals excepting the brow where it is apparently caused by the presence at that point of the circumorbital wart. The eyebrow in man is in reality a stripe which tends to pass backward in obedience to the tendency of the stripe in animals generally.

But the direction taken by the eyebrow is not a guide to all the transitions in the form of the black about the eyes. A vertical black stripe extends from the eye to the mouth in the cheetah (*Cynæurus jubatus*). The same patch includes the lip in some Newfoundland and pointer dogs.

The auricle and the hair growing from it need not be entirely black. The margin only is black in the hoary bat (*Atalapha cinerea*) and in *Didelphys*. The hair upon the auricle may be entirely white instead of black as in the North American badger (*Taxidea americana*). The base of the auricle may be alone covered with black hair as in the fox-terrier, or with tan as in the beagle.

The auricular black in the dog may include the skin of the side of the head for a variable distance and may cross the vertex and be in common with the corresponding patch of the opposite side. This arrangement interrupts the dorsi-facial white stripe. The appearance of black, tan or white spots on the vertex surrounded by patches of a contrasted color form "points" of breeding in some of the varieties of the dog.¹

May it not be expected that a connection can be traced between the region of the obelion and the pineal eye? Embryology teaches that the presence of various color marks of the skin appear before many of the more important deeper organs, and that the species to which an embryo belongs can be determined before the genus. The occasional reappearance in the dog of a patch of pigment at the spot at which an organ of special sense appeared in a remote ancestor, but which has no functional expression in the living descendant, is in harmony with many of the conclusions drawn from the data presented in this paper.

The Sides of the Body.—In *Pecora* the sides of the abdomen and chest are variously stripped and spotted when the body elsewhere, is differently marked. The young of the boar (*Sus scrofa*) is striped on the body. Lateral stripes are also seen in *Coelogenys*, and in *Tamias* and *Spermophilus*. Many varieties of domestic cattle show white spots extending up from the sides of the body from the ventre to variable distances.

Is it likely that the dorsal marks of the horse and carnivores, and the saddle marks of *Thyalcinus*, extending as they do downward are opposed in *Pecora*² by the disposition of ventral marks which extend upward?

Nerve-Endings.—The white stripes on the face in many South American bats, in *Lophiomys*, in *Taxidea*, and in some varieties of *Mephitis*, appear to be distinct from the simple contrast of color of

¹ In a recent exhibition of dogs in Philadelphia the vertex spot of the contrasted color was seen in the pointer, the Irish setter and the beagle each twice, in the spaniel and fox terrier each once.

² An exception is seen in *Antelope scriptus*, which has white saddle marks.

the black of the special organ above mentioned. In the tiger's marks, as seen on the muzzle, they are undoubtedly correlated to the distribution of the infra-orbital nerves. It is probable that similar patches of color, either black or white, are related to similar causes. Among them may be mentioned the black oral angle in *Felis onca*, the white lips of *Tapir pinchaque*, and the black lower lip in some varieties of the bull terrier and the fox terrier. In the ground hackie (*Tamias striata*) I have demonstrated that the main longitudinal body stripe answer to the terminal filaments of the intercostal nerves and to those nerves which are in serial homology with them.¹ I have found the spots on the fawn of the Virginian deer (*Cariacus virginianus*) answer to the places at which the cutaneous nerves pierce the fascia.

The papilla on the flexor aspect of the fore-arm which is seen in the domestic cat, the sciurmorph and myomorph rodents, and in some of the lemurs, is furnished with bristle-like hairs with the exception of the last named animals. It is supplied by a separate nerve in the domestic cat. The length of the hairs correlate with the length of the vibrissæ of the labial set, and are used (as I have observed in the common mouse) for cleansing the face and especially in combing the labial bristles. J. Bland Sutton² found a small bristle-bearing wart on the flexor surface of the the fore-arm in *Lemur catta*, *Chirogaleus coquerli* and *Hapalemur griseus*. No special pigment patches or hair clumps have been found associated with this papilla.

The so called "chestnut" of the fore-leg of the horse is probably homologous with this growth. Owing to the changes in the limb coincident with the reduction of the toes the growth assumes a more posterior position.

All warts and skin caruncles are best developed on the naked spaces at or near the margins of hairy surfaces. They are well seen on the margins of the regions of the whisker and the moustache in the human subject. They are found about the mandibles in the moose (*Alces canadensis*) and the hog. The same positions are seen occupied by warts in the bat where the face is sparsely haired. P. Michelson³ found warts on the margins of the pilose patches in *trichosis circumscripta*.

¹ Science 1887.

² Proc. Zool. Soc. Lond. 1887, 372.

³ Virchow's Archiv. 1885, C, 66.

Animals which are uniformly furred carry occasional warts on the face—one of these is always supra-orbital and another is on the cheek, and forms in the dog the so-called “kiss mark.” It is often separately marked by tan in the black and tan terrier, when it constitutes a “point” for the breeders of this animal.

Virchow¹ expresses the opinion that retention of lanugo upon the face may be confined to the distribution of the fifth pair of cranial nerves.

Muscle-Regions.—The stripes and spots on the limbs and the dapple-marks on the trunk, as well as some of the broader sheets of color, appear to be related to the intervals between muscle-masses or to the extent of skin-surfaces which corresponds to muscles.

The depression between the radial and digital extensors in the Felidae is often marked by a black stripe. *Felis chaus* of India according to Sir W. Elliot² exhibits a brown bar on the inside of the arm. This writer assumes that the mark is distinctive of the East Indian species. I have seen a black mark in the same locality, in many examples of the varieties of the domestic cat in or near Philadelphia.

The black mark on the front of the thigh in lemurs (see p. 93) is limited distally to the region of the tibia at which the gracilis, semitendinosus and sartorius muscles are inserted. The region of the back which answers to the lower trapezius sheet is abruptly outlined in pure black, in contrast to the white color of the loin and of the lower distal region, in *Indris brevicaudatus*.³ H. Ranke⁴ reports a case of *trichosis circumscripta*, in which a patch was found in front of and below the right knee and a second over the front of the left knee. These marks may be held to be homologous with the distal ends of the black femoral stripe in *Indris brevicaudatus* as already stated above.

Regions which are rich in Seba and Moisture.—Eschricht⁵ called attention to the fact of the early appearance of the sebaceous glands in connection with the development and distribution of the hair. While the presence of seba is found associated with hair-growth the fact that some clumps of hair are found in regions which are especially rich in the secretions poured from the skin, form a

¹ Berliner Klin. Wochenschr. 1873, No. 29.

² Darwin, An. under Domestication. Eng. Ed. I. 44.

³ Am. Mus. No. 260.

⁴ Archiv. f. Anthropologie, 1883, taf. XIII.

⁵ Müller's Archiv. 1837, 44.

separate group of the localities which show special disposition to retain abundance of hair. Such regions are illustrated by the hairy warts about gular pouches, by the hair of the axilla, of the pudenda and of the perineum.

The hair of the perineum is commonly distinctly colored in the dog and in some of the lemurs. The highly colored and vascular surfaces of the region of the perineum in the Cynopithecoids are probably created by the same cause.

The hair of the external auditory canal is associated with ceruminous glands. The coarse hair at the base of the nipple may be included in the same category.

I have found the wrinkles of the skin of the head of the wart-hog (*Phacochoerus aethyopicus*) correspond to the black stripes seen in the zebra (*Equus zebra*). I have no proof, however, that this marking is caused by influence of seba or of moisture.

The roof of the mouth being black in many mammals induces the observer of pigment patches to include this region under the heading of the distribution of color marks on the general integument. It is interesting to note that the efforts of breeders to run out the black from the integument will often result in the loss of pigment from the roof the mouth. That the oral surface is capable of yielding special outgrowths which are comparable to those of the skin is shown in *Balaena* and many rodents.

4. EFFECTS OF AGE.—That the color marks of young animals frequently differ from the adult forms is a matter of common observation. The relations existing between the young of one species and the adult form of others have been often observed but need further elucidation. The white collar at the base of the neck in some dogs is seen in the young form only of the bear. The change in the Himalayan rabbit from white, to white with dark markings has been already noted.

The corresponding changes which take place in the animal in old age has received much less attention than it deserves. The few observations I have made confirm the statements made elsewhere respecting the orientation of pigment patches. Horses often become gray in the circumpalpebral regions before they change elsewhere. An Italian gray-hound, which I have observed for a number of years, displays as it advances in senility a dorsal white stripe, a white star on the breast, a circumpalpebral gray patch and

white feet. In a word the fawn gray of adult life turns to white in the same regions (with the exception of the tip of the tail and the tip of the ear) that an animal is apt to break from its prevalent color. (See p. 88)

The loss of hair from the crown in man is the loss of the dorsal part of the "collar" of the *Quadrumana* as already mentioned on p. 95.

The growth of the hair from the tragus in man is more decided in middle life than at an earlier period and turns gray at a later period than the whisker.

5. **BILATERALITY.** The study of color marks in connection with the law of asymmetry yields many attractive results. Prof. Wm. H. Brewer¹ found the white marks on the feet of horses more developed on the left than the right side. In *Nyctipithecus* I have found the left supra-orbital region white, and a white spot detected on the left cheek, while the remainder of the fur was gray. H. Ranke² describes a case of *trichosis circumscripta* in which a pilose patch was seen on the left cheek in advance of the region of the whisker but none corresponding to it on the right. The left arm, according to R. Hilbert,³ may be alone pilose and a patch of ichthyosis be confined to the shoulder of the same side. Dr. Henry H. Donaldson found as the result of many observations on the human subject in the south of Germany, the wart on the nasio-labial groove to be much more frequent on the left than the right side. He found a similar disposition in numbers of engraved portraits of distinguished men of all nationalities. I have frequently found the black circumpalpebral patch in the fox-terrier and the bull-terrier confined to the left side, or when the patches are found on both sides the left patch to be the larger. According to W. H. Flower⁴ the color-marks of *Lycan* are remarkable for being different on the two sides of the body. Prof. Brewer states⁵ that in man the beard commonly turns gray first on the left side. It cannot be a coincidence that the left side in all the above instances shows the greatest disposition to variation. I have found a similar disposition to exist in the antlers of the Virginian deer.

¹ Proc. Am. Assn. for Advancement of Science 1881, XXX, 246.

² Archiv. f. Anthropologie 1883, XIV, 339.

³ Virchow's Archiv. 1885, XCIX, 569.

⁴ Article "Mammalia" British Encyclopedia, IX edition.

⁵ l. c. 249.

Naevus bearing abundant growths of hair has been found by J. Nevins Hyde¹ confined to the left side of the body in the form of three bands which followed in the direction of the intercostal nerves; a fourth band extended from the perineum to the scrotum and penis.

6. ANTERO-POSTERIOR ASYMMETRY.—The anterior half of the body may be disposed with reference to the color marks and the quantity or kind of hair, in a manner different from the posterior. This disposition is strikingly seen in many specimens of the tapir, the anterior part (with the exception of the lips which are white), being dark, while the posterior is white. In *Hystrix* the posterior half of the body alone bears the quills. In *Phascogale* the posterior half of the body is white. In *Hapale bicolor* a similar coloration is seen. In *Chrysochloris aurata* the posterior half only of the body justifies the name.

Concluding Remarks.—In reviewing the subject of the distribution of color marks in mammals it is evident that the causes of the arrangements are various, and do not admit of easy solution. The points which I have attempted to elucidate do not invalidate biological principles already established, while it must be acknowledged that some of them do not remain explained by these principles alone. That variations of deep lying structures will influence the periphery which over-lie them is a well established law. Illustrations are seen in the relations which exist between the true organs of generation and the skin coverings over them. It is but another application of the principle to find the sacral spot correlating to conditions of the neuro-enteric canal, and yet another in the skin about the nostril, the eye and the auricle remaining black because the true organs of olfaction, vision and audition also contain black pigment. The principle of antero-posterior symmetry—of bilateral symmetry and asymmetry are also illustrated.

The general contrasts of the color marks of the head as opposed to those of the body, which are so common in parti-colored animals, may be explained by the enormous influence which the brain must exert over the nutrition of the entire region. That nerve-endings can influence the color of the integument near them is abundantly proven. From the lateral line of teleostean fishes to the ground hackie is a long series in which the influence of nerve endings on the sides of the trunk can be associated with color marks. Sebaceous

¹ Chicago Med. Journ. and Examiner, Oct. 1877.

secretion and sweat conjoined with elevation of temperature appear to explain the retention of hair at the pudenda and axilla. Dr. Geo. Dinmick of Cambridge, Mass., has informed me that he has influenced the arrangement of color marks on the elytra of *Coccinella* by varying the temperature to which the insects had been subjected. According to H. Pryer¹ "temperature has a great evolutionary value in insects."

That margins of nutritive regions afford the conditions favorable to the appearance of warts agrees with what is known in a osseous system with respect to erosions and absorption. In a growing cranial bone I have found its greatest thickness in the position of its centre of ossific deposit; in the adult bone the thickness is greatest at the margins. When sutures are well defined vascular activity is most marked along their lines. In atrophy an area of deficiency always occurs lying at a point somewhere between the centre of ossification and the borders of the bone.²

It is probably in obedience to the same law that in baldness a lock of hair commonly persists at the bregma and in the upper part of the metopic line. With respect to skin folds it must be said that the disposition is caused primarily by the position of the skeleton of the limbs to that of the trunk, head and neck. In *Rhinoceros* and *Armadillo* the folds answer pretty exactly to the divisions above named. But the folds on the side of the trunk between the limbs in *Armadillo* appear to be caused by muscular action if one can accept the conclusions drawn from the appearances seen in the instantaneous photographs of the hog as taken by Mr. Muybridge.³

If motion can originate skin folds it can also determine color-regions, and the category of the pigment patches in the intervals between muscle-masses and the limitation of color-areas to muscle sheets become practicable.⁴

The history of each mammalian embryo must present many phases of nutrition—especially of precocity and of retardation—which determine individuality. In a litter of two or more individuals the changes due to temperature, to motion, to rate of local blood inter-

¹ Trans. Ent. Soc. Lond. 1882, 489.

² Am. Journ. Med. Sci. 1870, 405.

³ Photographs issued under the auspices of the University of Penna, series 673.

⁴ It is a tempting subject for study to elucidate the distribution of skin diseases by the application of the same methods undertaken in this essay. The margins of the areas of the lanugo,—the course of distribution of nerves or of vessels, the influence of the bone lying in close juxtaposition to the skin, the

change must cause variations in the rates of growth in accesion or repression of force which will call into activity one or more of the proclivities above named. The extreme variety of this individual experience doubtless explains the great difference seen in the ways that animals are colored.

The fact that coloration is limited, or that it is apt to be limited, to the points of convergence of Eschricht and Voigt would appear to be a tentative conclusion. The careful study of the peculiarities of the animals which are born naked would probably greatly strengthen it.

I will conclude by making the suggestion that the distribution of color-marks along the directions already indicated is a larger phase of the subject of evolution than is outlined by "mimeticism" and by "natural selection." I assume that *Ailuropus* does not, for the reason that it cannot, change the black feet, the black auricle and the black circum-ocular region for one in harmony with the ground color, notwithstanding the disadvantage to which the contrast between the black and white subjects him. I also assume that the breeders of the dog cannot run out the black from the skin over the sacrum and the root of the tail with the same ease he can determine many other colors. According to natural selection and domestication the various regions above named explain the frequent occurrence of colors which are of great use to the individual but they often meet with abrupt limitation owing to the influence of deep-lying restraining causes.

occurrence of acne pustules or syphilitic papules in positions in which the marginal warts occasionally appear,—the retention of the hair near the bregma and at the occiput in instances of loss of hair other than from age, can be noted in studying the distribution of eruptions upon the skin and of naevi as well as of color marks. But the field of observation is difficult when the conditions are often so fleeting. The impressions of a single observer are not sufficient to secure definite conclusions: For information, including literature of this phase of the subject, the reader may refer to the experimental researches of A. Irsai and V. Babesin¹ upon the influence of the nervous system upon the pathological conditions of the skin, and to T. S. Dowse on the nervous affections of the skin and its appendages.²

¹ Vierteljahresschr. f. Dermatol. u. Syphil. 1882, IX, 433.

² Med. Press and Circular 1879, I, 499.